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The influence of temperature and soil moisture on the population density of *Cognettia sphagnetorum* [Oligochaeta: Enchytraeidae] in cultures with homogenized raw humus[1])

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With 3 figures

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1. Introduction

The influence of temperature and moisture on the population density has been studied intensively on a number of terrestrial animals (e. g. Andrewartha and Birch 1961). These studies have in general been carried out on animals living above the ground. Soil animals have only been sparsely investigated. However, the variation in temperature and moisture is much less below the ground than above it. The relative humidity of the air in soils at the "wilting point" (pF ca. 4.2) is for example almost 99% (e. g. Kohnke 1968 p. 42, Rapoport and Tschapek 1967). According to Nielsen (1959) "the activity of small soil animals is largely confined to pF values below 4.5 ...". This means that a decrease in the relative humidity of the soil air of ca. one per cent is fatal for many soil animals. Therefore, special studies must be carried out in order to understand the influence of these factors on the population density of soil animals.

The effect of soil moisture on the population density of enchytraeids has been studied in field conditions by several authors (Nielsen 1955, O'Connor 1957, Nurminen 1967, Abrahamsen 1972). Nielsen (1955) found that lower moistures than values corresponding to pF 4 caused extermination of the populations. Below pF 3 on the other hand the enchytraeid activity did not seem to be influenced by the moisture. In a previous study (Abrahamsen 1972) it was similarly found that the threshold value for existence of enchytraeids seems to be slightly below 10% of the water-holding capacity at pF 0.5. In the following the water-holding capacity at pF 0.5 is designated WHC. A positive correlation between population density and moistures varying from ca. 10% to ca. 30% of WHC was also demonstrated. These observations, however, have never been confirmed by laboratory experiments which can be carried out with greater precision.

The influence of temperature seems to be less examined than soil moisture. Reynoldson (1943) studied the fecundity of *Enchytraeus albidus* Henle, 1837, and *Lumbricillus lineatus* (O. F. Müller, 1774) and recorded optimum temperatures between 15° and 20 °C. Sauerlandt and Marzusch-Trappmann (1959) on the other hand, mentioned that the optimum temperature "der Entwicklung von" *Enchytraeus buchholzi* Vejdovsky, 1879, is between 25 and 28 °C.

The main objective of this laboratory study was to examine the influence of soil moisture and temperature on the abundance of *Cognettia sphagnetorum* (Vejdovsky, 1877). This species dominates the enchytraeid populations in coniferous forest soils in

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1) A contribution from the Forest Soil Fertilization Research Group, 1432 Vollebekk, Norway.

Fennoscandia (Nurminen 1967, Abrahamsen 1968, 1972) and reproduces itself mainly by fragmention.

2. Material and methods

The growth medium used in this study was homogenized raw humus originating from a *Myrtillus* spruce forest type. The raw humus was dried at 50 °C to kill the enchytraeids present in the material. Higher drying temperature made the material unsuitable for the test animals. After drying, the raw humus was homogenized and sieved through a 2 mm sieve. Ten grams of this material, corresponding to 9.2 g oven dried material, were placed into jars of ca. 150 m*l*. After the humus was given the correct moisture, 10 individuals of *C. sphagnetorum* were transferred to each jar.

The jars were stored in incubators at 6, 12, and 18 °C. The variation in temperature was less than ± 0.5 °C.

The effect of moisture was examined in two experiments. In experiment I the following moistures as percentage of the water-holding capacity at pF 0.5 (WHC) were used: 7, 30, 50, 70, and 95 %. The WHC was determined as previously described (Abrahamsen 1972). Due to the results of experiment I, the following moistures were used in experiment II: 13, 19, 25 and 115 %. The moisture were maintained by adjusting the weights with distilled water two times a week.

It is probably more informative to give the moisture content as some unit of water potential e. g. pF. This study was, however, partly carried out to examine some of the results obtained in th previous study (Abrahamsen 1972) in which measurements of moistures expressed as pF was not successful and the soil moisture was given as percentage of WHC. In the present study, however, pF determinations were carried out. The relation between pF and the gravimetric water content in per cent of oven dried material or in per cent WHC is given in Fig. 1. The relation to the volumetric water content can be found as the specific gravity of the homogenized raw humus was ca. 0.23.

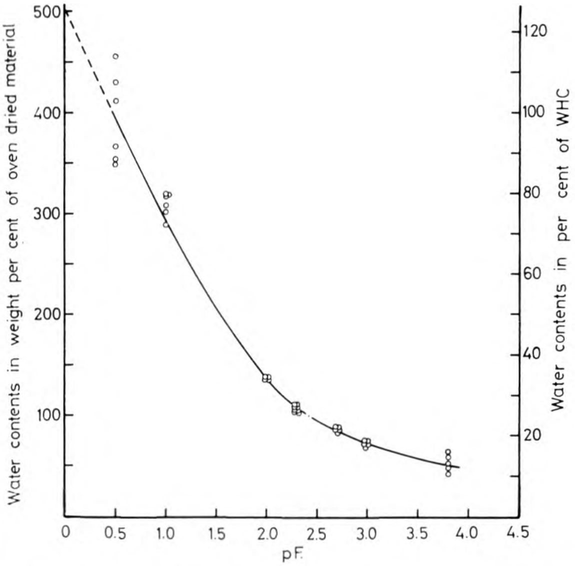

Fig. 1 The relation between pF and the gravimetric water content in per cent of oven dried material or in per cent of the water-holding capacity at pF 0.5 (WHC)

The jars were stored in the incubators in one, two, five and eight months. After these periods the humus in each jar was extracted separately in modified BAERMANN funnels (O'CONNOR 1955). The humus was used only once.

In these factorial experiments two replicates were used. Therefore, experiment I and II consisted of 120 and 96 jars respectively. The statistical analysis of the results involved that the mean squares of the different treatments had to be compared with the same residual mean square. To reduce the effect of the correlation among the mean square ratios the significant F-values were corrected as recommended by OTTESTAD (1970).

3. Results

In the statistical analyses the results for the 7 % moisture (pF > 4.5) were excluded since no individuals survived in these cultures (Fig. 2). The results of the initial analyses of variance carried out revealed that all main factors (temperature, moisture, observation period) and their interactions had a significant effect on the abundance of *C. sphagnetorum*. Further analyses showed that the significance of the interaction between temperature and moisture varied with the observation period (Fig. 2). This must be the reason for the significant three factor interaction observed in the initial analyses.

Both experiments revealed that the effect of moisture on the population density depended on the temperature. At 6 °C small differences were found among the moistures, but at 12 and especially 18 °C the differences were highly significant.

The effect of temperature was also related to the moisture. Below ca. 20 % of WHC (pF 2.8) temperature may be less important than moisture, and 12 °C seemed for example to be a more favorable temperature than 18 °C. The critical value below which no enchytraeids could survive was between 7 and 13 % of WHC (pF ca. 4).

Above ca. 20 % of WHC on the other hand it seemed to be a quadratic relation between temperature and abundance. A regression analysis carried out on the data from the five months observation period in experiment I showed that the relation between temperature and abundance at this moment is described by the function $y = 204.2 - 51.9\,t + 3.51\,t^2$ where y is the abundance and t is the temperature. This function is based on moistures from 30 % to 95 % of WHC. The great effect of temperature can also be illustrated by the average monthly growth in the first five months. At 6 °C the average monthly increase was 1.8 and 0.5 individuals in experiment I and II respectively. At 12 °C the corresponding figures were 15 and 12, and at 18 °C 79 and 47 individuals. The highest monthly growth recorded in any culture was 210 individuals.

According to experiment II the optimal moisture was between 25 % and 115 % of WHC. Experiment I revealed further significantly higher abundances after one month in the cultures with 50 % and 70 % moisture (pF 1.5—1.1) than in the other cultures. After two months however, the highest abundances were found in the cultures with 70 % and 95 % moisture (pF 1.1—0.6). For the first two observation periods no interaction was found between temperature and moisture. Longer observation periods led to a decrease in the optimal moisture at 18 °C. At 6 and 12 °C the optimum still seemed to be between 50 % and 70 % of WHC. However, the reduction in optimal moisture at 18 °C was not real, but caused by a reduction in the WHC of the humus material. This reduction was observed after five to six months by the appearance of free water in cultures at 18 °C with 95 % and 115 % water contents. This means that the moistures probably in all cultures have increased considerably from the original moistures.

The results obtained in this study also give information on the growth rate of populations of *C. sphagnetorum*. The growth depended mainly on temperature and moisture,

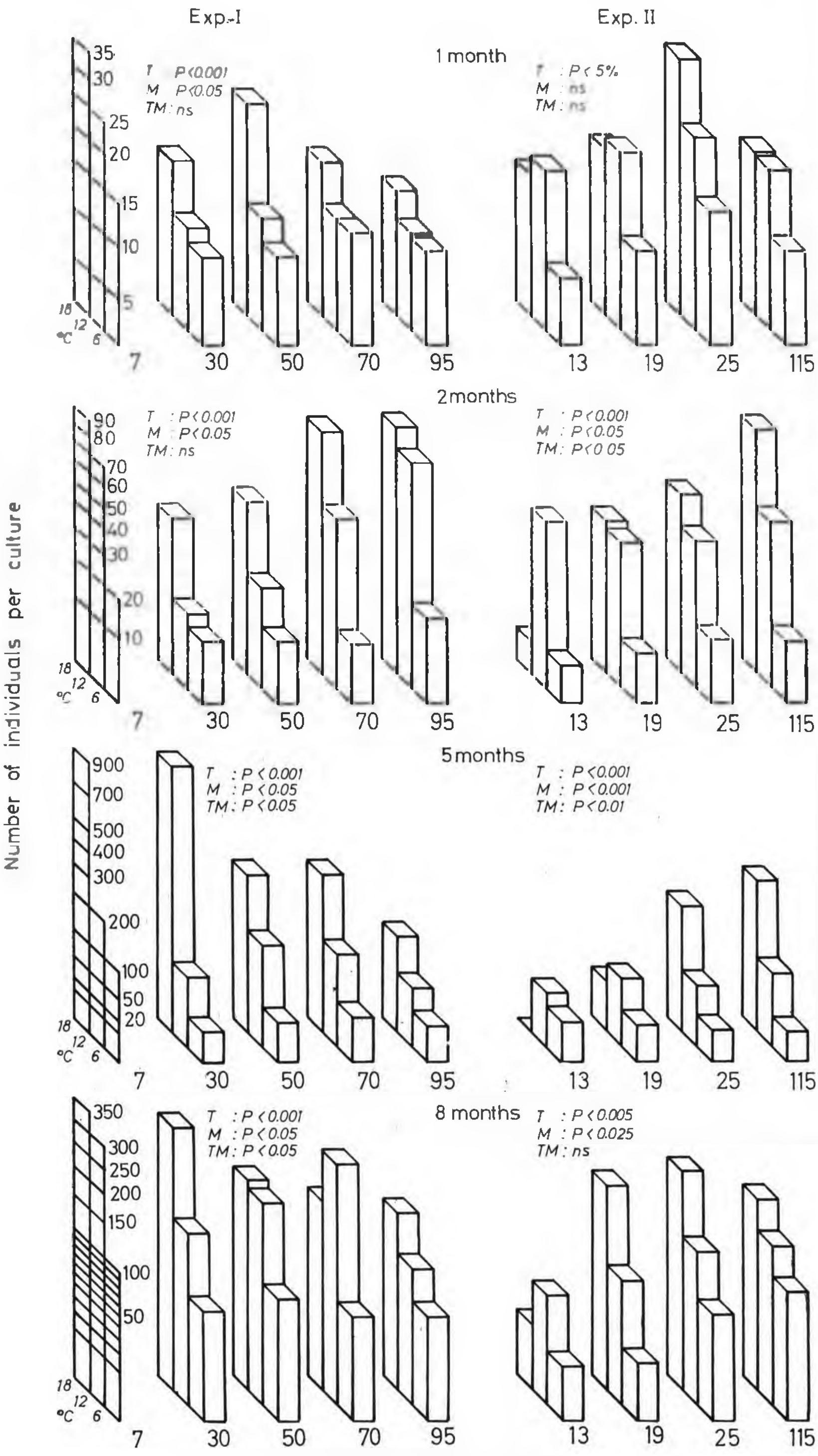
Exp.-I
Exp. II
Number of individuals per culture
1 month
T P<0.001
M P<0.05
TM: ns
T : P < 5%
M : ns
TM : ns
35
30
25
20
15
10
5
18
12
°C
6
7
30
50
70
95
13
19
25
115
2 months
T : P < 0.001
M : P < 0.05
TM: ns
T : P < 0.001
M : P < 0.05
TM: P < 0.05
90
80
70
60
50
40
30
20
10
5 months
T : P < 0.001
M : P < 0.05
TM: P < 0.05
T : P < 0.001
M : P < 0.001
TM: P < 0.01
900
700
500
400
300
200
100
50
20
8 months
T : P < 0.001
M : P < 0.05
TM: P < 0.05
T : P < 0.005
M : P < 0.025
TM: ns
350
300
250
200
150
100
50
Soil moisture in per cent of WHC

Fig. 2

Fig. 2 The abundance of *Cognettia sphagnetorum* at different temperatures (°C), soil moistures (% of WHC), and observation periods (months). (T) Effect of temperature; (M) Effect of moisture; (TM) Interaction between temperature and moisture; (ns) Not significant

but to reduce the number of growth curves all moistures except 7 % in experiment I were grouped. In experiment II only the data from 25 and 115% moistures were used. For each experiment and each temperature the regression between the abundance and the observation period was estimated (Fig. 3).

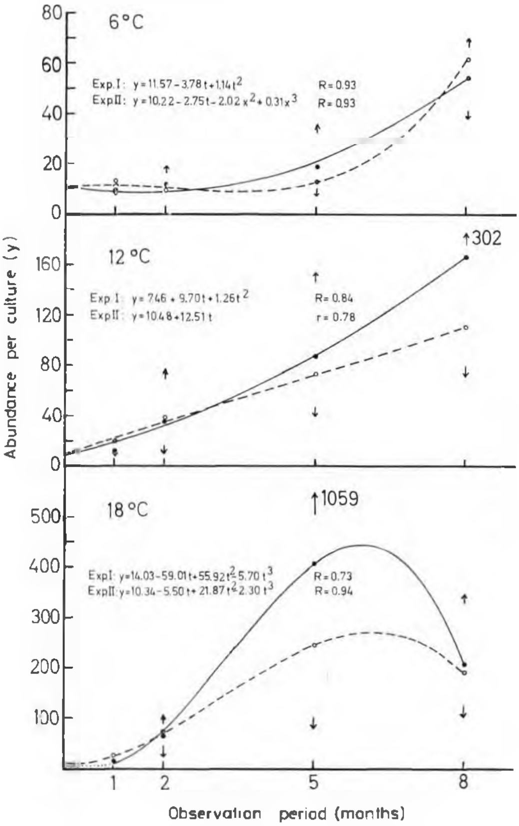

Fig. 3 The abundance of *Cognettia sphagnetorum* in relation to observation period and temperature. Experiment (I) solid line, df = 38; Experiment (II) broken line, df = 18. ↑ and ↓ = highest, respectively lowest abundance observed per culture in experiment I

All growth curves show similarities to the logistic curve, but the latter does not decrease as do the curves of 18 °C. At this temperature the average maximum population density was probably reached after ca. six months.

4. Discussion

The abundance of *Cognettia sphagnetorum* obtained in the two experiments was not compared directly as the origin of the raw humus material was slightly different. This involved for example that the amount of nitrate- and amonium nitrogen was twice as high in the humus used in experiment I compared with the humus of experiment II.

It can be concluded that *C. sphagnetorum* was unable to survive in soil where the water was retained with greater forces than ca. 10 atm. (pF ca. 4). This supports the conclusion of NIELSEN (1955) as previously mentioned. In the raw humus material used in the present study pF 4 corresponded to ca. 10 % of the water-holding capacity at pF 0.5 (WHC). Therefore, this observation also supports a conclusion previously made on the threshold moisture for *C. sphagnetorum* in raw humus of coniferous forest soils (ABRAHAMSEN 1972).

Very high moistures did not seem to restrict the abundance of *C. sphagnetorum* to any great extent. In the present study decreasing WHC involved cultures saturated with water, but the abundance in some of these cultures reached ca. 6500 individuals per dm³. This number is ca. six times greater than the highest abundance previously recorded in natural raw humus in Norway (ABRAHAMSEN 1972). The low abundances recorded in peat (ABRAHAMSEN 1972) is therefore, hardly due to excess of water. Most microarthropod populations seem according to VANNIER (1970) to be more impeded by excess of water than by a deficit.

The high tolerance against excessive water may be the reason for the high optimal moisture observed for the population growth in the first two months. After five and eight months observation period the WHC of the raw humus material had decreased most probably as a result of the decomposition of the material. Considering Fig. 1 it will be seen that the water content in saturated humus (pF ca. 0) was approximately 120 % of the WHC. This may indicate that the real water contents in the cultures have increased from 95 % to at least 120 % of WHC. Therefore, the optimal moisture seemed to be independent of the observation period. To some extent it seemed also independent of temperature, but at 6 °C the moisture was much less important than at 12° and especially 18 °C. The conclusion therefore, is that water contents corresponding to pF 1.5 to 0.6 (or for the raw humus material used in this study 50 %—95 % of the WHC) gave maximum growth of populations of *C. sphagnetorum*. This conclusion is supported by a previous observation where a significant positive correlation was found between the abundance of *C. sphagnetorum* and the soil moisture when the moisture varied between 10 and 30 % of the WHC (ABRAHAMSEN 1972). In the previous study a conspicious parallel variation was also observed between the relative vertical distribution of different enchytraeid species and the soil moisture when the moisture varied between ca. 40 and 80 % of the WHC. The present results are however, not in agreement with NIELSEN's (1955) observations where moistures above those corresponding to pF ca. 3 did not seem to influence the population densities. There may be several reasons for this discrepancy. For the first, it is easier to observe small effects in laboratory experiments than in field experiment where a variety of factors influence the population densities. Secondly, different species are involved in the two studies. In NIELSEN's study *Fredericia bisetosa* (LEVINSEN 1884) was the dominating species.

The growth curves show the average growth at moistures varying from ca. pF 2.4 to pF 0. As the optimal moisture corresponded to pF values from 1.5 to 0.6, this means that the growths shown in the figure were not maximal. The difference from the maximal growth was most pronounced at 18 °C as the moisture was most important at this temperature. The highest population density obtained in the experiments corresponds to ca. 24,000 individuals per dm³ while the corresponding average density (18 °C, experiment I) was ca. 9,500 individuals per dm³. IVLEVA (1953) recorded population growths at 18—20 °C for *Enchytraeus albidus* which was much faster than observed in the present study. In the course of ca. two months one of her populations increased ca. 70 times while 10 times increase was the highest noticed during a two months period in the present study. The quantity of soil used in Ivleva's study was, however, not given. She also added food to the cultures and a real comparison of the growth rates is, therefore, difficult.

Any definite reason for the decreasing abundance after ca. six months in the present study and after ca. two months in Ivleva's study cannot be determined. Ivleva mentioned the accumulation of metabolic products as one reason. Shortage of food may, however, have been more important in the present study as no fresh food was added to the cultures during the experimental period.

In the previous study (Abrahamsen 1972) comments were made on the significant increase in population densities of Enchytraeidae from Finland through Norway and Denmark to England. This increase seems reasonable when considering the effect of varying moisture and especially varying temperature reported in the present study.

5. Acknowledgements

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6. Summary

(1) The threshold moisture below which individuals of *Cognettia sphagnetorum* are unable to survive corresponded to ca. pF 4 or to ca. 10% of the water-holding capacity at pF 0.5 (WHC) of the raw humus material used as culture medium.

(2) The worms were not seriously reduced in numbers when the raw humus got saturated with water.

(3) The moisture where maximum abundance was obtained corresponded to pF values between 1.5 and 0.6 or 50 to 95% of the WHC.

(4) The growth curves for the abundance were similar to the logistic growth curves, but at 18 °C the abundance decreased after an observation period of ca. 6 months.

(5) The relation between temperature (from 6 to 18 °C) and the growth in abundance seems to be described by a quadratic function. After five months observation period and moistures varying from pF = 2.1 to pF = 0.6 the abundance had increased from 10 individuals per culture to 19 at 6 °C, 86 at 12 °C and 406 at 18 °C.

6. Zusammenfassung

(1) Die kritische Feuchtigkeitsstufe unter der Individuen von *Cognettia sphagnetorum* nicht überleben können, entspricht etwa pF 4 oder etwa 10% der Wasserkapazität bei pF 0,5 (WHC) von Rohhumusmaterial, das als Kulturmedium verwendet wurde.

(2) Die Abundanz der Würmer wurde nicht ernstlich reduziert, wenn der Rohhumus mit Wasser gesättigt wurde.

(3) Die Feuchtigkeit, bei der höchste Abundanzen erzielt wurden, korrespondierte mit pF-Werten zwischen 1,5 und 0,6 bzw. 50 bis 95% der Wasserkapazität (WHC).

(4) Die Kurven des Anstiegs der Abundanz waren ähnlich wie logistische Wachstumskurven, aber bei 18 °C ging die Abundanz nach einer Beobachtungsperiode von etwa 6 Monaten zurück.

(5) Die Beziehung zwischen Temperatur (von 6—18 °C) und dem Anstieg der Abundanz läßt sich anscheinend durch eine quadratische Funktion beschreiben. Nach einer fünfmonatigen Beobachtungsperiode und Feuchtigkeiten, die zwischen pF = 2,1 bis 0,6 variieren, stieg die Abundanz von 10 Individuen pro Kultur auf 19 bei 6 °C, auf 86 bei 12 °C und auf 406 bei 18 °C.

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